CARNIVOROUS PLANT NEWSLETTER

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Front Cover: *Drosera cistiflora* at Baines Kloof. See article on page 42.

Back Cover: *Nepenthes danseri* growing in laterite gravel. See article on page 50.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Contributors should review the "Instructions to Authors" printed in the March issue of each year. Advertisers should contact the editors.Views expressed in this publication are those of the authors, not the editorial staff.

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Contents

Board Member Elections

The end of this year will mark the end of terms of office for at least three ICPS board members. We will be saying goodbye to Madeleine Groves, Joe Mazrimas, and Rick Walker. Madeleine is finding her career too demanding to allow her the time to be a board member. Joe is going to be spending more time on his other pursuits, including growing plants and travelling. Rick Walker, ex officio president, is also ending a term in accordance with our bylaws. The remaining board members extend their thanks to these officers for the work they have done for the ICPS.

If you are interested in running for a board position in the ICPS, please send a 250 word election statement to Barry Meyers-Rice or Jan Schlauer (contact information is on the inside cover of Carnivorous Plant Newsletter). Your election statements must be received by 1 August, 2000. In your statement, you may wish to note your experience, why you want to run for office, and what you wish to accomplish. Your statements will be printed in the September issue.

The ICPS is a growing, active organization. In order to participate as a board member, email access is essential. Furthermore, board members are expected to work hard! So while we welcome and encourage your interest as a board member, remember that it is more than a vanity post. Consider running for office—your energy is appreciated and needed!

Looking Back: CPN 25 Years Ago

"Fred Case has formally described what he feels is a new and distinct species, *Sarracenia alabamensis*. These plants occur in disjunct locations in central Alabama and are quite rare, tending to decrease almost yearly in their natural habitat due to the sort of land misuse we who do field work are all too well aware of." Twenty-five years later, Fred is still active in *Sarracenia*—he just co-authored a paper describing a new species of pitcher plant, *Sarracenia rosea*!

Peter Prager wrote about his new method for mealy-bug control, in which he "rinsed them well and then submerged them in distilled water for five days to hopefully drown any remaining insects and eggs.... There have been no bugs in the three months since I submerged the plants. The plants did not seem to suffer from the submergence (except *D. pulchella*, which rotted) and in fact, I have been treated to an added bonus. Very shortly after transplantation, many of the *Drosera*, including *D. adelae* and *D. hamiltonii* began producing tiny plantlets all over their leaves and now my collection of *Drosera* has virtually doubled in number!!!"

HELIAMPHORA HISPIDA (SARRACENIACEAE), A NEW SPECIES FROM CERRO NEBLINA, BRAZIL-VENEZUELA

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Keywords: new taxa: Brazil, *Heliamphora hispida*, Venezuela.

Received: 2 February 2000

Introduction

Cerro Neblina is the southernmost tepui of the Guyana Highlands at the Brazil-Venezuela border. Recently discovered in 1954, surrounded by extensive rainforests and very difficult to reach, it remains one of the least explored regions in the world. Due to its isolation, it exhibits the highest degree of plant endemism of all the tepuis. In December 1998, a group of carnivorous plant enthusiasts (Fernando Rivadavia, Prof. José Maurício Valéria Piliackas, Ed Read, Gert Hoogenstrijd, Christoph Scherber, Dr. Kathrin Hinderhofer and the authors) began an expedition to study the carnivorous plants of Cerro Neblina (for details on this expedition see Rivadavia, 1999). Besides locating the previously known *Heliamphora tatei* var. *neblinae*, we also discovered a new *Heliamphora* species which is clearly different.

Heliamphora hispida Wistuba & Nerz *spec. nov.*

Caudex ramosus; foliis rosulatis; amphoris 15-20 (a. 25) cm longis, ventricosis; orificiis expansis infundibuliformibus; parallele plurinervibus et transversim reticulato-venosis, extus glabris, parte superiore interiore ciliata; appendice cucullato 1-1.5 cm longo, 1-1.5 cm lato, cordato, basi constricto; inflorescentiis 3-5-floris, racemosis, ad 50 cm longis; flores nutantes; pedicellis 5 cm longis; petalis 4 oblongo-lanceolatis, albidis val pallide-roseis, 5-6 cm longis; staminibus 10, 1-serialibus, filamentiis 7 mm longis; antheris oblongo-lanceolatis, ca. 7 mm longis; ovario valde tomentoso; stylo glabro; stigmate 3 lobato; seminibus fuscis, oblongis, ca. 2-3 mm longis, testa conspicue membranaceo-alata.

Rhizomes branching, plants forming dense clumps with age. Pitchers slightly ventricose in the lower half, broad-infundibulate and expanded in the upper part, 15-20 cm, occasionally up to 25 cm long, 5-8 cm wide in the upper part, pitchers greenish with red veins, in exposed habitats dark red; the upper half of the pitchers densely ciliate in their interior, cilia variable, occasionally up to 4 mm, middle part of pitcher glabrous, basal part coarsely ciliate; lid cordate, strongly narrowed at the base, 1-1.5 cm long, 1-1.5 cm wide, with an appendage, 1-1.5 mm long on the outside near the tip; inflorescence about 50 cm long, peduncle glabrous in the lower part, slightly pubescent in the upper part; pedicels 5 cm long; bracts ovate 4-5 cm long, bearing rudimentary pitchers; tepals, 4, oblong-lanceolate 5-6 cm long, 2-3 cm wide, white to whitish-pink; 10 stamens in 1 series, filaments 7 mm long, anthers oblong-lanceolate, approximately 7 mm long, 1.5 mm wide; ovary 3 celled, pubescent, style glabrous; seed approximately 2-3 mm long, compressed, ovate, irregularly winged.

Specimens Examined

Heliamphora hispida : Cerro Neblina 01/01/1999 Wistuba et Nerz No. Neb 01.01.99/1, holotype, flowering plant (VEN).

Heliamphora hispida : Cerro Neblina 01/01/1999 Wistuba et Nerz No. Neb 01.01.99/2, flowering plant (VEN).

Etymology

The name is derived from the Latin "hispidus" (bristly) after the coarse cilate hairs on the interior pitcher surface of some individuals.

Distribution

So far, *Heliamphora hispid*a is only known from the southeast end of Cerro Neblina. It is remarkable that *Heliamphora tatei* var. *neblinae* is found very scarcely in this area, probably due to different habitat requirements. In the northeast part of Cerro Neblina, *Heliamphora tatei* var. *neblinae* grows in huge highland meadows associated with *Brocchinia reducta*. *Heliamphora hispida* is the only *Heliamphora* that grows in meadows around Pico Phelps. According to one reference this species has been seen once before in an adjacent area: Charles Brewer-Carias (1987) shows several photos of such plants (pages 209 and 210) without any explanations in the text. Brewer-Carias mentions that the plants had been photographed at the Titirico River, approximately 7-8 km northeast of Pico Phelps. It seems that *Heliamphora hispida* is the dominant species in the southeastern part of Cerro Neblina.

Ecology

Heliamphora hispida grows at Cerro Neblina, usually in bogs and highland meadows. It is quite common on highland meadows below Pico Phelps, and even at the very top of Pico Phelps (3014 m) some clumps of *Heliamphora hispida* can be found. Usually it is not associated with *Heliamphora tatei* var. *neblinae*, which we have found only in an open meadow east of Pico Phelps. Here, *Heliamphora tatei* var. *neblinae* was found growing closely with but clearly separated from *Heliamphora hispida*, which grows in shady spots on open shrubby bogs. It is remarkable that plants frequently grow partially submerged in these habitats, so that the water level inside of the pitchers is approximately the same as in the surrounding substrate. In that area, we also found another curiosity: a cluster of debris (consisting partially of decayed leaves and rhizomes of *H. hispida*) fully 1.80 m in height and totally overgrown with *H. hispida* plants. The southeastern end of Cerro Neblina is mostly covered in low forests, or swampy areas with low shrubs and dominated by *Bonnetia* and other montane shrubs and treelets. Other areas are dominated by *Brocchinia tatei*. These areas are not suitable for *Heliamphora tatei* var. *neblinae*, which prefers flat open meadows at altitudes of 1800-2000 m. It seems that *Heliamphora hispida* is better adapted to grow in the shrubby areas in the southeastern part of Neblina and at higher altitudes (1800-3014 m) with their colder and harsher conditions.

Hybrids

We found one small population of hybrids, possibly consisting of stabilized hybrids between *Heliamphora hispida* and *Heliamphora tatei* var. *neblinae*. The pitchers of these plants were quite long and tubular, almost as in *Heliamphora tatei* var. *neblinae*, but the lid was small and round as in *Heliamphora hispida*. Just a few of these plants were found growing between dense shrubs. It is interesting that neither *Heliamphora tatei* var. *neblinae* nor *Heliamphora hispida* were growing close to this population.

Relation to Other Species

Heliamphora hispida is clearly distinct from all other known *Heliamphora* species (*Heliamphora tatei*, *Heliamphora nutans*, *Heliamphora heterodoxa*,

Heliamphora minor and *Heliamphora ionasii*; Bentham, 1840; Gleason, 1931; Maguire, 1978; Steyermark, 1984). Apparently it has closest affinities to *Heliamphora minor* and *Heliamphora ionasii*. *Heliamphora hispida* shows distinct differences in the shape of pitchers, the lid, and in details of the flowers compared to *Heliamphora minor*. *Heliamphora minor* is usually somewhat smaller than *Heliamphora hispida*. *Heliamphora ionasii* is different because of its huge dimensions in all parts of the plant, besides differences in the shape of pitchers and details in flowers as can be seen in Table 1.

	Heliamphora hispida	*Heliamphora minor*	*Heliamphora ionasii*
Pitcher			
Dimensions	15-25 cm long 5-8 cm wide	8-20 cm long 3-8 cm wide	40-50 cm long 10-15 cm wide
Shape	Slightly ventricose in the lower part, broad-infundibulate and expanded in the upper part	Slightly ventricose in the lower part, narrowly expanded to tubular in the upper part	Ventricose in the lower part, highly expanded in the upper part
Lid			
Dimensions	1-1.5 cm long 1-1.5 cm wide	0.5-1 cm long 0.3-0.5 cm wide	2-3 cm long 2-3 cm wide
Shape	Cordate, curved	Strongly "helmet"-shaped	Cordate, curved
Inflorescence			
Dimensions	Peduncle 50 cm long pedicels 5 cm long	Peduncle 20-40 cm long pedicels 3-4 cm long	Peduncle 100 cm long pedicels 12 cm long
Tepals			
Dimensions	5-6 cm long 2-3 cm wide	4-5 cm long 1.5-2.5 cm wide	3.5-6 cm long 2-3.5 cm wide
Shape	Oblong-lanceolate, narrowing near the base	Lanceolate, broad base	Lanceolate, broad base
Anthers/Stamens			
Dimensions	7 mm long	4 mm long	3.5 mm long
Number	10	15	15

Table 1: Comparison between *Heliamphora hispida*, *Heliamphora minor* and *Heliamphora ionasii*.

Discussion

Until now, only one *Heliamphora* species with long, tubular pitchers was known from the southern tepuis (*Heliamphora tatei* var. *tatei* from Cerro Duida, Cerro Huachamachari and Cerro Marahuaca; *Heliamphora tatei* var. *neblinae* from Cerro Neblina and Cerro Aracamuni). Species with more compact or short pitchers (*Heliamphora nutans, Heliamphora minor, Heliamphora heterodoxa* and *Heliamphora ionasii*) were only known from the eastern tepuis (e.g. Roraima Tepui, Auyan Tepui, Ptari Tepui or Ilu Tepui), which are separated by a distance of some 600 km from the western tepuis. *Heliamphora* is not known to occur between these areas. Therefore, it was thought that this division into tubular pitchered "western species" and compact pitchered "eastern species" was due to geographic isolation because of long distances between these areas. Now for the first time it can be seen that this separation is not valid. *Heliamphora hispida* clearly has morphological affinities to the "eastern species" such as *Heliamphora minor* or *Heliamphora ionasii*, and is clearly different from the known "western species."

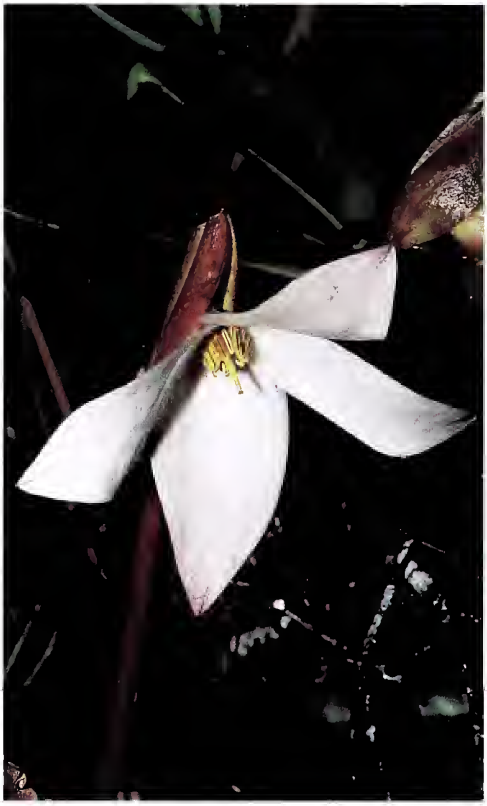

Figure 1: *Heliamphora hispida* flower. Photograph by J. Nerz.

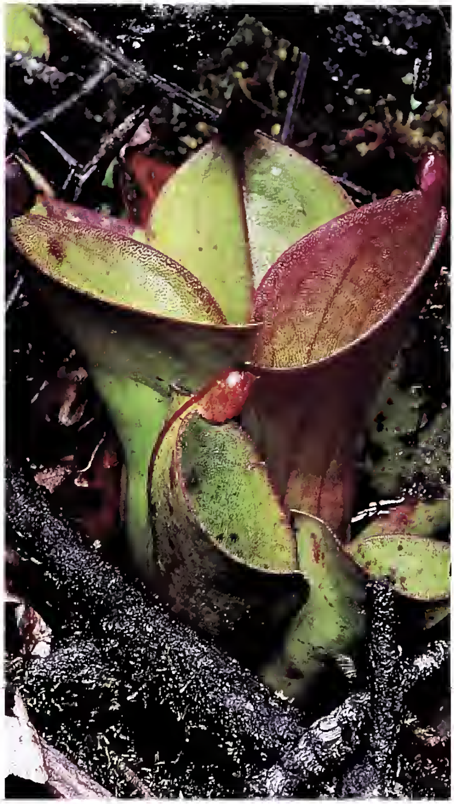

Figure 2: *Heliamphora hispida*. Photograph by A. Wistuba.

Figure 3: *Heliamphora hispida* habitat. Photograph by A. Wistuba.

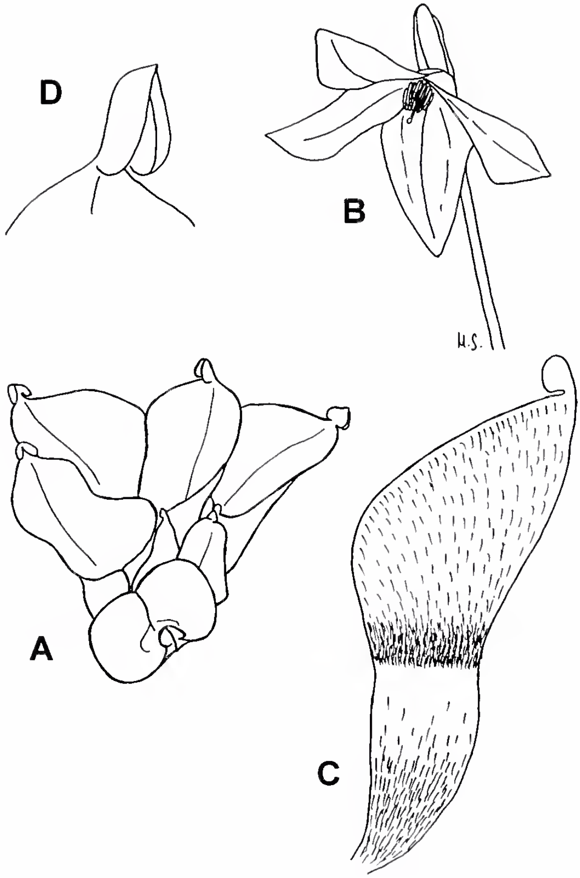

Figure 4: *Heliamphora hispida* Wistuba et Nerz; A. Vegetative part of plant (×1/2); B. Flower (×1); C. Trichomes on the inner pitcher surface (×1); D. Lid (×3). Drawing by Matthias Schmidt.

Acknowledgements

We wish to thank our Brazilian friends Fernando Rivadavia, Prof. José Maurício Valéria Piliackas for giving us this great opportunity to visit Cerro Neblina. Without them this expedition would certainly not have been possible. We also thank Matthias Schmidt for his excellent line drawing.

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Endless Carnivorous Plants in Cape Town, South Africa

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Keywords: travelogue: *Drosera*, South Africa.

From late August to early October 1997, I travelled around southern Africa in search of adventures and carnivorous plants. In Africa, just about everything that could have happened did happen, both good and bad. I was robbed almost as soon as I arrived in Johannesburg (all my money, documents, new camera, etc.), spent two weeks with Eric Green in Cape Town during which I saw endless carnivorous plants all around south-western South Africa (including the magnificent *Drosera cistiflora* and *D. pauciflora*, with amazingly large flowers which come in practically all colors), gave a talk to the South African Carnivorous Plant Society, saw beautiful carnivorous plants in the Pretoria/Johannesburg area, all the while taking in the amazing adventures, sights, and sounds that Africa presents. This is an account of the carnivorous plants I saw during the time spent with Eric Green and family, as I recovered from the scary experience of the robbery in Johannesburg.

Eric did a great job of helping me forget my troubles, taking me all around to see the best carnivorous plant locations he knows, showing me some of the most beautiful *Drosera* species known. I also discovered that the Cape Town region has some of the most beautiful scenery in the world, with magnificent sandstone highlands and escarpments spread all around. I was amazed at how the local fynbos vegetation was similar to the Brazilian "campo rupestre" vegetation on the mountains back home. The plant species may be different, but the general aspect is very similar—short bushy plants and lots of grasses. The geology is apparently identical: sandstone highlands with lots of seepages and streams, the water tainted reddish-black with tannic acid, and sandy soil often blackenned by organic matter and ashes from previous years' fires. Even the climate is very similar, although Cape Town's winter is slightly longer. The main difference with Brazil is that the rainy and dry seasons are reversed—in Cape Town the winter is the rainy season and summer is the dry season.

My introduction to carnivorous plants in Africa was at Eric's house, where I drooled over his fantastic collection. Simply amazing! I saw *D. cistiflora* in flower for the first time (Figure 1) — but this was only a taste of what we would later see in the wild. I had never before seen many of the other South African species he had in his collection, nor so many mature, flowering *Heliamphora* species. Another first for me, a total knockout, was his giant and fully mature seventeen-year-old *Nepenthes rajah*! I did not even know there were any of that size in cultivation!

It was interesting that the lowland carnivorous plant habitats I saw in the Cape Town area were very similar to the carnivorous plant habitats I remember from Western Australia! The most common plants in the African habitats were *D. cistiflora*, *D. pauciflora*, *D. zeyheri*, and *D. trinervia*, members of section *Ptycnostigma*. Just like those in Western Australia, these species go dormant during the summer dry season. Instead of surviving the dry season as corms, they rely simply on thickened roots which store water and carbohydrates.

Drosera from the section *Ptycnostigma* also occur in the highlands, in habitats which apparently dry out faster than the habitats occupied by other *Drosera* species. This reminds me of the Brazilian species *D. hirtella*, *D. colombiana*, and *D. montana* var. *montana*, which also grow in relatively dry habitats, and how they survive the dry season as dormant roots.

The first places Eric took me to see wild carnivorous plants was the Silvermine Nature Reserve and then Red Hill near Simonstown, both near Cape Town. We saw *D.*

cuneifolia, *D. glabripes*, *D. hilaris*, *D. ramentacea*, *D. aliciae*, *D. zeyheri*, *D. admirabilis* (?), *D. cistiflora*, and *D. trinervia*. Nine *Drosera* species in only a few hours! I still have not gotten over the giant flowers of *D. cistiflora* and *D. pauciflora*—up to seven centimeters in diameter! And what amazingly beautiful colors too! They varied from white to purple to red to pink to light-yellow. My favorite was the *D. cistiflora* with deep-red petals. I noticed that the *D. cistiflora* still had their flowers open around four or five pm at one site. I wonder if this is common for the sect. *Ptycnostigma* species? I also noticed that *D. pauciflora* has large tentacles on the tips of its leaves like *D. burmannii*, and like the fast-moving tentacles of *D. burmannii*, these bend over in a few seconds when stimulated.

Among the many beautiful mountain passes I travelled through while exploring South Africa, my favorite was Baines Kloof, which I visited twice. In addition to fantastic views, it houses vast numbers of carnivorous plants. This is the only known location of *D. regia*, the longest-leaved of all *Drosera*. I hiked all around, saw numerous carnivorous plants (including the narrow-leafed form of *D. capensis*, which is not nearly as weedy in the wild as it is in cultivation) and *D. cistiflora* (see Front Cover), but absolutely no *D. regia*. Comparing notes with Eric later, I discovered that I had trampled right through the *D. regia* site, but did not see them. I had been looking for long leaves in an open habitat, but learned from Eric that they actually grew in thick grasses and that the leaves were still not too long because the plants had just recently broken out of dormancy. Oh well, perhaps next time...

Another very interesting place was Hermanus, a bit further south along the coast from Cape Town. Hermanus is a famous whale-watching spot, but unfortunately there were no whales on the day I went. Nevertheless, the carnivorous plants compensated well for their absence. I was alone again, following Eric's instructions and maps. Yet no matter how detailed the instructions, it is usually very difficult to describe how to find a specific natural location (as I discovered with *D. regia*!). Fortunately, I had no problems and found all the carnivorous plants I expected to see and even more!

D. cistiflora with white to light-pink flowers and white-flowered *D. trinervia* were spread all around Hermanus. Another very common species was the beautiful *D. glabripes*, which has reddish spoon-shaped leaves on stems around 10-15 cm high (see Figure 2), reminding me somewhat of *D. chrysolepis* back home. I even found two specimens of the rare hybrid *D.* × *corinthiaca*. Its leaves were very similar to those of *D. glabripes*, but it formed no stem.

Probably the most amazing carnivorous plant in the Hermanus area was *D. slackii*. According to Eric, they were not so large at that time of year, but the color of the plants monopolized my attention. They were entirely colored a beautiful deep pink-red, including the stipules. The shape of the leaves is unique, as is the presence of the numerous, thick dark-red hairs on the underside of the leaves.

I also found what Eric said were *D. curviscapa* and *D. esterhuysenae*, both considered synonymous with *D. aliciae* by Jan Schlauer in his carnivorous plant database. I do not know if the names are correctly applied here, so it would be better for me to describe what I saw. The *D. aliciae* had reddish-green compact rosettes, leaves pressed flat on the ground, and grew in wet to humid areas in the semi-shade of grasses. The *D. curviscapa* (?) grew in drier sandy soil, often semi-shaded by other plants, and bore larger green semi-erect leaves. *D. esterhuysenae* (?) also grew in drier sandy soil, but under full sunlight (Figure 3). Its leaves were an orangish-green color, flat on the ground, and with huge tentacles at the tips, like those of *D. pauciflora* and *D. burmannii*. I do not know if *D. curviscapa* and *D. esterhuysenae* should be considered distinct species, but they surely seemed to be distinct taxa from *D. aliciae* and probably deserve at least subspecific or varietal status.

Another plant seen at Hermanus was *Roridula gorgonias*. Although no longer considered carnivorous, it is nonetheless a very interesting species. The *R. gorgonias* were less than a meter in height, since fires had killed the larger ones a few years back. But there were many plants and it was fantastic to observe those bugs which live on the leaves, crawling around unimpeded by the sticky glands, feeding on the captured insects. At Eric's collection I experimented placing these bugs on *Drosera*, *Drosophyllum*, and *Pinguicula* and found out to my surprise that they could crawl around just as easily on these struc-

turally similar carnivorous plants, although on the first two the bugs became coated with mucilage.

Unexpectedly, I also found what appeared to be a possibly new, "floating" species of *Drosera* at Hermanus, which Eric only knew from Baines Kloof. It was growing in a very wet spot by a stream together with what later proved to be a large-flowered *U. bisquamata*—strangely, the only *Utricularia* I saw while in the Cape Town area. Although very boggy, this site was not flooded, and the floating *D.* sp. were stemless, small rosettes flat on the soil surface. A few months later, my friend Rob Gibson from Australia passed by this site. He believes these small plants are actually *D. admirabilis*.

Eric also took me to a place in the Cedarberg Mountains, a few hours north from Cape Town, where he showed me numerous *Drosera* species. We also saw blooming *Roridula dentata* reaching almost two meters in height, and at one site it formed a very dense and large stand. The most interesting carnivorous plant that day was probably *D. alba*, which grew by the thousands on thin layers of mosses over bare rocks in very wet spots along streams. In the dry season these sites become bone-dry according to Eric, and like other section *Ptycnostigma* species, *D. alba* survives as dormant roots. The most curious characteristic of this species is its dimorphic leaves, a characteristic also observed in *D. cistiflora*. The first leaves to appear in the wet season form a small rosette similar to that of *D. trinervia* or *D. aliciae*, although of a deep wine-red color. Then suddenly the leaves begin growing erect and string-shaped, like a young *D. filiformis*. The flowers are small and white.

At the Cedarberg Mountains, Eric also showed me a possibly new variety of *D. cistiflora* which he attributes to Günter Eitz. These plants have very short stems, and the basal rosettes are made of long, semi-erect leaves similar to those of *D. adelae*, instead of the usual flat rosettes with shorter *D. trinervia* or *D. aliciae*-like leaves. The flowers are also a unique lilac color, with the edges darker than the center. Nevertheless, I suspect all these differences may be due to ecological factors. This *D. cistiflora* is very similar to the local form of *D. cistiflora*, which is also short-stemmed.

To top off that day, we found a single unique specimen which seemed to belong to the *D. cistiflora*-complex. It had a small rosette with tongue-shaped leaves below a few younger, narrower, longer leaves. But what caught our attention the most was its flower, which was a dark pink-red, a color which Eric claimed to have never seen among South African *Drosera*. I think it was possibly just a genetic or ecological freak, emblematic of how variable *D. cistiflora* can be, but Eric thinks it might be something new.

The *D. cistiflora*-complex is truly absurd in its variability. The differences observed in leaf size and shape, stem length, flower size and color, all show that this is a taxon undergoing heavy speciation. Maybe a million years from now it will be several different species, but at the moment all I could see was one huge gradient with no clear boundaries, and no possibility of dividing it into discrete subspecies or varieties. The only taxon in the *D. cistiflora*-complex which possibly deserves distinction is *D. zeyheri*. This is considered by some taxonomists to be no more than a stemless form of *D. cistiflora*. I saw *D. zeyheri* at two or more sites in the Cape Town area and it appeared to me to be a valid species, easily distinguishable from *D. cistiflora*, although it does sometimes have one to three leaves on the flower scape.

I still find it hard to believe that in only two weeks I saw approximately fifteen *Drosera* species! I guess the only other place in the world where this is possible is Western Australia. But even more amazing than the number of species was their tremendous abundance and incredible beauty. I really do not know how to thank Eric and his family for the fantastic time I had with them in Cape Town, for showing me all around, and especially for having helped me get over the robbery in Johannesburg and all the troubles I had in obtaining a new passport, visas, plane ticket, credit card, money, etc. Thank you Eric!

(*The editors thank Robert Gibson for the use of his photograph of* Drosera esterhuysenae *from the Highlands. Fernando tells us the plants in the photograph look much like the ones he saw in Hermanus.*)

Figure 1: *Drosera pauciflora* with a flower 7 cm in diameter, Darling South Africa.

Figure 2: *Drosera glabripes* at Hermanus.

Figure 3: *Drosera esterhuysenae*. Photograph by Robert Gibson.

New Cultivars

Keywords: cultivar: *Pinguicula* 'Hanka', *Sarracenia* 'Abandoned Hope', *Sarracenia* 'Lamentations', *Sarracenia* 'Spatter Pattern'.

Pinguicula 'Hanka'

Submitted for registration 25 November 1999.

The novelty is a hybrid selected from offspring made by the author in 1990 by crossing *Pinguicula zecheri* Speta & Fuchs (female plant) and *P. rotundiflora* Studn. (male plant). The selected cultivated variety, nominated by the author in 1992, forms a winter succulent rosette and a summer carnivorous one, both relatively small and rather brown-coloured when grown in sunny sites. The winter rosette, consisting of about 50 drop-shaped leaves, measures about 27 mm across. The summer rosette, consisting of 10 to 18 leaves, measures about 45 mm across. Its leaves are spathulate, membranous, turned upwards in the margins.

Flowers are produced at any time, by both the winter and the summer rosettes, but most frequently in November. Flower stalks are about 55 mm high. The corolla is subisolobous, is oval in outline when viewed from the front, and measures up to 30 by 27 mm. The wide corolla lobes touch or cover each other in the margins. They are corrugated and slightly emarginate. The corolla is lilac, darker reticulated, with a yellowish stripe in the middle lobe of the lower lip. The corolla tube is 4 mm long. The bluntly pointed spur is 8 mm long, bent towards the lower lip. The calyx consists of narrow, about 2.5 mm long lobes, rounded at the tip. The calyx, the corolla tube, the spur and the flower stalk are endowed with glandular hairs.

The stigma is purple, corrugated, with long hairs in the reverse side. The plant is sterile. Its minor capsule measures 1 mm, and it is spherical, dark green, with sessile glands on the surface. *Pinguicula* 'Hanka' may be propagated easily by means of leaf cuttings made from the numerous winter leaves. It is cultivated in the Botanical Garden Liberec (see please the address below) at the present time. It has been sent also to Japan.

The described cultivated variety is dedicated to my daughter Hana P. ("Hanka" in a familiar name form), as nice as the described flowers and to my pleasure also clever in botany.

—Miloslav Studnička • Botanic Garden Liberec, Purkyňova 1• 460 01 Liberec • Czech Republic

Sarracenia 'Abandoned Hope'

Submitted for registration on 15 January 2000

I created this *Sarracenia* × *catesbaei* in 1989 by crossing *S. purpurea* subsp. *venosa* var. *burkei* with *S. flava* var. *flava*. This notable cultivar was distinguished from its siblings by having enormous early season pitchers, particularly when its flowers are removed at an early stage. While similar to other *S.* × *catesbaei* crosses using similar varieties of the two parent species, this individual stood out by attaining pitcher heights as great as 80 cm (30 inches). Only one or two spring and early

summer pitchers of this enormous size are produced, and the pitchers that follow later in the season are only about half this size. Also notable is the oversized, wavy and undulating lid that can effectively reduce collected rainfall and thus lessen the toppling nature that plagues *Sarracenia × catesbaei*. The pitcher body is olive-green with red longitudinal veins both straight and jagged, plus lesser horizontal veins joining those that run lengthwise along the pitcher. The ala is pronounced along the lower half of the pitcher and edged in red. The red lip of the mouth is held horizontally. A prominent red splotch at the throat radiates red veins throughout the yellow-green lid. The flowers are large-petaled and peach-pink on the exterior surface, beige on the inner surface.

I coined the name in 1994. The name is taken from the sign at the entrance to Hell in Dante's Inferno: "Abandon All Hope, Ye Who Enter Here." This cultivar should only be reproduced by vegetative means.

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Sarracenia 'Lamentations'

Submitted for registration on 15 January 2000

This plant has narrow, upright trumpets 30-45 cm (12-18 inches) tall and no more than 2.5 cm (1 inch) wide at the mouth. The olive-green pitchers are heavily veined with dark red nerves; when grown in full sun, the upper two-thirds of each pitcher, including the lid, turn entirely reddish-maroon with especially dark veins (unlike the individual in the photograph). The back of the pitcher throat, and underside of the lid, can turn dark purple-burgundy. This cultivar is especially notable for the upper inclination of the lid, which is wider and longer than the mouth opening. The lid has slightly wavy margins and fine bristles on the underside. The pitchers are notable for lasting well into the winter dormant season in good condition. The flowers are small, with dark red 2.5-3.5 cm (1-1.5 inch) petals, similar to *Sarracenia rubra*, and are borne on stems as long as the pitchers. The flowers are slightly fragrant, similar to cherry flavored drinks or roses.

The origins of this plant are something of a mystery. It is possible it originated from California State University at Fullerton in the 1980s. In any event, I coined the cultivar name in 1995. The name notes how the clusters of pitchers, with their upturned lids, can metaphorically appear to be crying towards heaven. This cultivar should only be reproduced by vegetative means.

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Sarracenia 'Spatter Pattern'

Submitted for registration on 15 January 2000

This plant has an unknown parentage, but it probably includes *S. leucophylla* and *S. rubra*. Its very narrow, upright trumpets average 38 cm (15 inches) tall and less than 2.5 cm (1 inch) at the mouth. The tumpets have a very slight bulge cen-

Figure 1: *Pinguicula* 'Hanka'

Figure 2. *Sarracenia* 'Abandoned Hope', photo E.M. Salvia.

Figure 3: *Sarracenia* 'Lamentations', photo Barry Meyers-Rice.

Figure 4: *Sarracenia* 'Spatter Pattern', photo E.M. Salvia.

tered 5 cm (2 inches) below the mouth lip (at least on full-sized pitchers). The ala is largest on the lower half of the pitcher, and is less than 1 cm (.5 inch) wide. The lid (finely hairy underneath) is inclined upwards, and flares to slightly wider than the width of the mouth. Its margins are undulate. The upper parts of the pitcher, including the lid, have a white background that is heavily veined red and laced with red-orange. Travelling down the pitcher tube, the red venation becomes even stronger and the dominant color. Below that, the lower half of each pitcher tube is dominated by green. The flowers are medium-sized with red petals up to 5 cm (2 inches) long. The scapes are up to 50 cm (20 inches) long.

I nominated the name in 1999. The name originates from a term used in criminal forensics, indicating a spray of blood used as evidence in a violent crime. This cultivar should only be reproduced by vegetative means.

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GROWING *NEPENTHES* IN A COMPLETELY INORGANIC SUBSTRATE

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Keywords: cultivation: *Nepenthes*, planting media.

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Introduction

Nepenthes are usually planted in mixtures incorporating organic matter such as peat, pine bark, *Osmunda* fiber, *Sphagnum*, *etc.* While these materials produce good results, they have disadvantages. Most of the ingredients decompose rapidly, and the result is a compressed substrate that inhibits air circulation among the roots. As a consequence the plants have to be repotted frequently. This means extra expense and work for the grower, and in almost every case, a temporary cessation in growth of the freshly repotted plants which lasts until the disturbed roots acclimatize. Another problem is that the use of peat directly contributes to destroying the wetlands where it is quarried. The destruction of habitat, in turn, is the main reason for the disappearance of many carnivorous plants. Because of these disadvantages, new planting media are always being sought.

In the wild, some *Nepenthes* species are found growing in inorganic soils. For a few examples, *N. danseri, N. neoguineensis*, and other species from New Guinea and the Philippines grow in lateritic soil (see Back Cover), *N. eustachya* grows in bare rock (Figure 1), *N. lavicola* thrives in volcanic rock, and *N. madagascariensis* lives in quartz sand. These observations suggest that it may be possible to grow *Nepenthes* in inorganic media.

Alternative Substrate

Rockwool is commonly tried as a non-organic planting material. In spite of limited success with some *Nepenthes* species, this method is not favoured because of health risks associated with handling this stuff. In two papers, Feßler (1982, 1986) described growing *Nepenthes* in lava-clinkers. He attributed his successes with lowland species to the available N, P_2O_5, K_2O and Mg the lava contains, and also to the fact that it has the ability to store up to 20% water by volume. From this description an alternative potting mix was developed, which works for all sixty *Nepenthes* species tested—lowlanders and highlanders alike. Even species such as *N. ampullaria* and *N. bicalcarata* do well, even though they often grow naturally in peat swamps.

Table 1. Advantages and disadvantages of the new inorganic potting mix.

Advantages	Disadvantages
1)Moistens easily, even when completely dry. 2)Compresses/degrades slowly (repotting is less frequent). 3)Airy mix is optimal for the roots. 4)No peat or *Sphagnum* is required, so habitat destruction is not promoted.	1)Heavy (adding one part Styrofoam chips may help). 2)Initial cost is higher.

The mixture consists of one part each: Seramis® clay perls (Effem, Verden/Aller), lava gravel (sold in aquarium shops, grain size approximately 1 cm),

and Lecaton® (expanded clay perls used for hydroponics, grain size approximately 1 cm) (Figure 2). These ingredients have the advantage of being more widely available than lava-clinkers. The mixture is slightly alkaline with a pH of 7.2, and should be soaked in purified water before being used.

Potting Plants with Inorganic Mix

The best pots are plastic baskets commonly used for cultivating water lilies. These baskets promote air circulation near the roots. They are available in square and round shapes, and the round ones are best used as hanging baskets. Conventional plastic pots may also used, especially for smaller plants.

The potting procedure is as follows. Remove the plant from its old pot, and remove all the old substrate from its roots by submerging it in a bucket of purified water. This decreases the chance of residual organic material, caught in the roots, of rotting. Put a layer of the potting mix in the new pot. Plant the specimen in the middle of the pot, filling the pot with the inorganic potting material. Immerse the whole pot in purified water, at room temperature. Plants grown in organic soil, repotted into the inorganic mix, show almost no interruption of growth.

Repotting plants already grown in inorganic substrate is even easier (although this is rarely a necessity!). The roots easily separate from the substrate, and are ready for repotting.

Watering can be done by immersing the entire pot, or from above until water drains from the pot. Both methods serve to provide the plant moisture as well as to leach accumulated salts out of the planting medium. As long as the pots do not sit in water, it is impossible to overwater them.

The water quality is of great importance. If your rainwater is polluted or contaminated, use reverse osmosis water.

Fertilization

It is necessary to fertilize your *Nepenthes* because this planting medium does not contain decomposing organic matter. Slow-release fertilizers such as Osmocote® 16-8-12(-2) (i.e. 8.3% N from NH_4 + 7.7% N from NO_3, 8% P from P_2O_5, 12% K from water-soluble K_2O and 2% Mg from MgO) are preferred. One third of the amount suggested on the label is enough for *Nepenthes*. The fertilizer is best mixed with the substrate before potting. At six-month intervals, add the same amount of fertilizer onto the top of the pot.

Propagation

Cuttings root exceptionally well in the substrate. They are directly planted in the substrate, (with or without rooting hormones), and are treated like rooted plants. If the cuttings have pitchers, add water to them. The substrate is too coarse to be used for sowing seeds. Use pure Seramis® or fine vermiculite instead.

The medium is very good for the acclimatization of sterile grown (i.e. tissue culture) *Nepenthes*. After removing the agar sticking to the plants, pot them in clear plastic boxes containing the substrate. Maintaining a relative humidity of almost 100% is most important during the first two weeks. Afterwards, the plastic cover is removed and the plants are treated like adult plants. Since the substrate can be autoclaved, the plants may be kept sterile or at least minimally contaminated by troublesome moulds during the beginning of this weaning procedure. Figure 3 shows a specimen of *N. sumatrana* two years after planting it out. When weaned it had a diameter of only 5 cm!

Figure 1: *N. eustachya* growing on bare rock.

Figure 2: The ingredients of the inorganic potting mix.

Figure 3: *N. sumatrana* growing in the potting mix.

General Conditions

The described results are all obtained growing *Nepenthes* in terraria of varying sizes with artificial lights (cool white fluorescent lamps or high pressure mercury lamps). Modifications of the methods described may be necessary to adapt them to greenhouse conditions. Nevertheless, hopefully many other growers are encouraged to experiment and report on their results in the future.

References
Feßler, A. 1982, *Nepenthes* in Lava-Schlacke, Dt. Gartenbau, 36, 1643-1644.
Feßler, A. 1986, *Nepenthes* in Lava-Schlacke, Das Taublatt, 3 (6), 6-8.

Literature Reviews

Cheek, M. & Jebb, M. 1999, *Nepenthes* (Nepenthaceae) in Palawan, Philippines, Kew Bull., 54: 887-895.

In this paper, the two taxa recently described (under the names *N. wilkiei* and *N. mira*) by the same authors are illustrated and discussed in more detail. Fortunately, original herbarium material of *N. philippinensis*, the type specimen of which was assumed destroyed at Manila during the Second World War, has been discovered at Kew. Unfortunately, the plant represented by this material is conspecific with the recently described *N. wilkiei*, making this name a later synonym. *N. philippinensis* is thus reinstated as a species distinct from *N. alata*, and the authors advocate the intriguing theory that it is more closely related to Bornean species, *viz. N. hirsuta*, *N. hispida*, and *N. macrovulgaris*. This is supported by a number of morphological and ecological similarities (e.g. like *N. macrovulgaris*, *N. philippinensis* grows on ultramafic soil). *N. mira* is maintained to be related to the likewise Bornean alliance containing *N. villosa*, *N. edwardsiana* and *N. macrophylla*. Recently discovered specimens (from further localities on Palawan island) that may represent unusual growth forms of the insufficiently known *N. deaniana* are considered in an additional note. The Philippines may thus yield further insights into long lasting *Nepenthes* secrets.(JS)

Clarke, C. 1999, *Nepenthes benstonei* (Nepenthaceae) a New Pitcher Plant from Peninsular Malaysia, Sandakania, 13: 79-87.

A new species of *Nepenthes* from Bukit Bakar, Kelantan, Malaysia, is described. Its most prominent features are a thick, glaucous cuticle, terete stems, and decurrent leaves. The rosette leaves bear brown hairs along their margins. The affinities of this rather distinct taxon are not entirely clear, and it is compared with *N. sanguinea* and *N. macrovulgaris*. Colour and black & white photographs complete the description.(JS)

Godt, M.J.W & Hamrick, J.L. 1999, Genetic Divergence Among Infraspecific Taxa of *Sarracenia purpurea*, Sast. Bot., 23: 427-438.

With allozyme analysis (comparison of numbers and sizes of different genes that code for proteins catalyzing a common biochemical reaction), the morphologically defined infraspecific entities recognized within *Sarracenia purpurea* have been established as genetically distinct entities. A grouping like (*burkii* (*purpurea* (*venosa*, *montana*))) was established, suggesting that a taxonomic reevaluation (especially of the status of var. *burkii*, which should perhaps better be excluded from subsp. *venosa*) may be warranted. Cultivated material of var. *montana* displayed a very low genetic diversity (the plants being practically clones of a single genetical individual), and it is recommended to supplement the cultivated population with propagules from further populations.(JS)

Naczi, R.F.C., Soper, E.M., Case, F.W., & Case, R.B. 1999, *Sarracenia rosea* (Sarraceniaceae), A New Species of Pitcher Plant From The Southeastern United States, Sida, 18(4): 1183-1206.

The attractive plant *Sarracenia purpurea* subsp. *venosa* var. *burkii* is well known to the readers of Carnivorous Plant Newsletter. (Before being described as a new variety, this plant was called the "Louis Burk" form by horticulturists.) This variety differs from other *S. purpurea* subsp. *venosa* plants because it has pink petals (instead of red), shorter flower peduncles, and slightly different pitcher characters. The authors of this new paper have decided that, based on these features, *Sarracenia purpurea* subsp. *venosa* var. *burkii* should be elevated to the status of a new species, *Sarracenia rosea*. As a result of this new species description, you may also see the anthocyanin-free plant *S. purpurea* subsp. *venosa* var. *burkii* f. *luteola* referred to as *S. rosea* f. *luteola* (a new combination made in this paper).

The authors present an interesting set of measurements, and demonstrate that there are consistent differences between *Sarracenia purpurea* subsp. *venosa* var. *burkii* and *Sarracenia purpurea* subsp. *venosa* var. *venosa*. However, it is not convincing these characters merit a new, separate species status for *Sarracenia purpurea* subsp. *venosa* var. *burkii*. Clearly, *S. purpurea* and *S. rosea* together form a pair of taxa that are extremely closely related, much more so than they are related to any of the other species in the genus *Sarracenia*. This argues for the relegation of *S. rosea* to an infraspecific status, as it occupies under the name *Sarracenia purpurea* subsp. *venosa* var. *burkii*.

While the new name *Sarracenia rosea* has been formally established according to the rules of the ICBN, it is not at all clear if this status is appropriate. It will be the choice of the botanical community to adopt it or to continue to use the name *Sarracenia purpurea* subsp. *venosa* var. *burkii*. Readers are encouraged to seek out the original publication and reach their own conclusions. (BAMR)

News & Views

Jedediah Brodie and Ch'ien Lee (Malesiana Tropicals, 1st Floor, Lot 4909, Sect. 64 KTLD, Uplands Shop House, Jalan Uplands, 93310 Kuching, Sarawak, Malaysia, jedediah_brodie@yahoo.com) reported interesting *Nepenthes* news: On 12 September 1999 we were examining several *Nepenthes* species on a roadcut near Kuching, Sarawak, and found the remains of a small rodent in a lower pitcher of a *N. rafflesiana*. The pitcher was 32.5 cm high. The mammal remains consisted of grey fur, two femurs, portions of a skull (including eight teeth and a jaw), and other bones. They were identified by Dr. Charles Leh, curator of mammals at the Sarawak Museum, as a *Mus* sp. The Asian house mouse (*M. castaneus*) is the only *Mus* species confirmed in Borneo, but it is usually only found near human structures. The rodent might also be a species of *Chiropodomys* (pencil-tailed tree mouse) which tend to live in tall or secondary jungle.

This find is notable because the only species of *Nepenthes* that has been recorded catching mammals is *N. rajah*, from Sabah. Anthony Lamb (*pers. comm.*) states that the rodents captured by *N. rajah* plants were found after periods of drought; the animals may have been attempting to drink out of the pitchers and slipped in. Similarly, we made our find following a two-week long dry spell in the region. *Nepenthes rafflesiana* has been recorded catching vertebrates such as geckos in Brunei (C. Clarke 1999, *pers. comm.*), but this is the first record of a captured mammal.

The roadcut site was relatively exposed, with secondary jungle and logging roads around its edges. Other species present were *N. gracilis*, *N. ampullaria*, *N. albomarginata*, *N. mirabilis*, *N. reinwardtiana*, *N. hirsuta*, and several natural hybrids.

Richard Ellis (1276 Cavan St., Boulder, CO 80303-1602, USA, ricell@juno.com) notes: I have been having fun growing sundews from the *Drosera petiolaris* complex. In general they seem to do well in the same environments as my lowland *Nepenthes*—they like it warm to hot. *Drosera paradoxa* seems to be a particularly easy to grow species. I have planted it in pure peat, 50:50 peat, and long fiber sphagnum moss, grown it inside under lights and outside in Colorado summers and none of these variables seems to matter to it. I was disappointed that many of the *Drosera petiolaris* complex plants did not make it into Lowrie's Carnivorous Plants of Australia, volume 3. Many of these species were in cultivation (and pictured in Carnivorous Plant Newsletter) before they were officially named, so I thought the following list might be useful for anyone who is trying to match new names to the old.

New Names	Old Names
D. brevicornis Lowrie	*D.* aff. *petiolaris* "Medium Rosette"
D. broomensis Lowrie	*D.* aff. *petiolaris* "Smooth Scapes"
D. caduca Lowrie	*D.* aff. *petiolaris* "Edkins Range"
D. darwinensis Lowrie	*D.* aff. *petiolaris* "Mini Rosette"
D. derbyensis Lowrie	*D.* aff. *lanata* "Derby"
D. dilatato-petiolaris Kondo	*D. dilatato-petiolaris*
D. falconeri Kondo & Tsang	*D. falconeri*
D. fulva Planchon	*D.* aff. *petiolaris* "Long Scapes"
D. kenneallyi Lowrie	*D.* aff. *falconeri* "Mitchell Plateau"
D. lanata Kondo	*D. lanata*
D. ordensis Lowrie	*D.* aff. *petiolaris* "Kununurra"
D. paradoxa Lowrie	D. aff. *petiolaris* "Erect"
D. petiolaris R-Br	*D. petiolaris*

Barry Meyers-Rice (P.O. Box 72741, Davis CA 95617 USA) had a near death experience: This fall I dropped in on a collection of plants I help steward at the University of California at Davis and was horrified to see that one of the *Pinguicula moranensis* plants—a specimen with tremendous horticultural potential—had rotted into muck. All the leaves were slimy and stringy at the base, and the plant looked like a horribly overcooked artichoke. In desperation, I completely dissected the plant and made leaf cuttings out of every piece of greenery that was still alive. Within a few days, all these leaf cuttings rotted away except for three succulent leaflets from near the center of the rosette. Just the other day I saw with joy that all three had started to produce plantlets! Saved from the grave! If I can manage to keep this plant alive, I will establish a cultivar name for it as soon as I can—the plant is that pretty! So the moral is, if your Mexican *Pinguicula* plant rots, take cuttings from everything you can—I never thought these would work, but they did.

Jean-Pierre De Witte (Oststrasse 8, D77866 Rheinau, Germany, j.dewitte@t-online.de) commented on germinating old *Nepenthes* seeds: I decided to clean out my refrigerator and get rid of the seeds I stored over time. So I prepared tissue culture-medium and started old *Nepenthes* seeds. The first to germinate after two weeks (with a rate of better than 80%) were highland seeds from 1996, but surprisingly highlanders from back in 1993 germinated (still better than 15%) after four weeks. So one should not despair—proper storage and germination technique do wonders.

THE ENDURING CONTROVERSIES CONCERNING THE PROCESS OF PROTEIN DIGESTION IN *NEPENTHES* (NEPENTHACEAE)

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Keywords: carnivory: *Nepenthes* — chemistry: *Nepenthes* — history.

Introduction

Plants typically make their protein using carbon incorporated from photosynthesis and nitrogen taken up from inorganic mineral in the soil. In contrast, animals, fungi and carnivorous plants make their protein—at least in part—from materials derived from the tissues and enzymes of other organisms. In these organisms, protein sources are broken down by enzymes, called proteases, into their basic building blocks, called amino acids, which are then absorbed. There is no doubt that tropical pitcher plants (*Nepenthes*) eat prey: they attract it, kill it and absorb the products of digestion. How *Nepenthes* accomplishes this process has been the object of study for 125 years. An enduring controversy with respect to *Nepenthes* digestion concerns whether the digestion is effected by proteases produced by the plant itself (endogenous) or from the activities of bacteria or other free-living sources in the pitcher fluid. In this review, I trace the history of this study, pointing to some of the major accomplishments in our increased understanding of the process and some of the important questions yet to be resolved.

The Early Years: 1874-1942

Inspired directly by Charles Darwin, J. D. Hooker (1874) was the first to document that *Nepenthes* is carnivorous. He established the digestive activity of the fluid, stating that egg-white, meat and cartilage all showed unmistakable evidence of disintegration within 24 hours. Others confirmed Hooker's observations on digestion and added the important observation that acidification increased the digestive activity (Gorup-Bensanez, 1874; Tait, 1875; Gorup-Bensanez & Will, 1876). Vines (1877) showed that extracts from the pitchers themselves could digest fibrin, but only when acidified. Pre-incubation of the pitcher with dilute acid increased the digestive activity. Evidence mounted that *Nepenthes* produces the digestive enzymes endogenously and that the digestive process is remarkably like that of our own stomach.

This theory was disputed first by Dubois (1890) in France and then by Tischutkin (1892) in Russia. Their two studies were similar in that they both found that the fluid of opened pitchers effected digestion, but that of unopened pitchers did not. While this was not a new observation (Tait had already noticed this in 1875), their conclusion was novel. They believed digestion was not accomplished by the secretion of the pitcher, but rather by the action of bacteria and infusia that gather in the opened pitchers. Goebel (1893) and Vines (1897) countered the bacterial hypothesis with additional evidence. Goebel showed that opened pitchers effected digestion even when bacteria were not present and that the fluid from unopened pitchers, when acidified, digested protein. Vines (1897) showed that fluid from unopened pitchers digested protein when 0.2% HCl was added. Acidified water, on the other hand, did not digest protein. Further experiments by Vines demonstrated that digestion occured even when bacterial poisons were present. Couvreur (1900)

claimed that Vines' results were due to the interaction of reagents, but he offered no rigorous support for his theory, nor were his arguments sound. In 1901, Vines suggested the name nepenthin for the *Nepenthes* digestive enzyme.

The relative importance of digestion by bacteria versus digestion by plant enzymes was still unclear. Goebel (1893) had suggested that plant enzymes dominated the digestion processes when the pitchers were young and the pH was low, but when the pitchers aged, the pH rose and microorganisms became responsible for more of the digestion. Vines (1877) had shown that extracts from young pitcher walls digested protein, but in older pitchers this activity was lost. Hepburn (1918) found that bacteria isolated from the pitchers could digest protein and that the colonies always causes an alkaline reaction.

Three studies in the 1930s filled out our picture of the role of endogenous versus microbial digestion. Stern and Stern (1932) tested the digestive activity of fluid taken from open pitchers with insects present, at different pHs. They found that the fluid generally had two optimal activities, one at a low pH and one nearer to neutral. When they tested digestion of albumin with pitcher extract instead of fluid, they found only one optimum at low pH. Okahara (1933) found that bacterial isolates from pitcher fluid were active against a range of proteins when tested in the pH range 6-8. At pH 3.3, however, none of these isolates degraded protein and most did not even survive. Some fungi isolated from the fluid, however, could still degrade protein at low pH. Zeeuw (1934) showed that if the fluid of open pitchers was kept sterile by use of bromine water and a cotton wool plug, the neutral pH optimum of digestion found by Stern and Stern was lost, suggesting it was derived from bacterial activity, and the low pH digestion was endogenous.

In 1942, Lloyd reviewed digestion in *Nepenthes* and concluded:

> As the matter stands at the present, therefore, the positive evidence that [an acid protease] is secreted by the pitchers of *Nepenthes* is conclusive. That...digestion in the absence of bacteria takes place there seems little doubt, but this cannot yet be said to be completely proven.

This statement marks the transition to the modern era, in which the focus is not whether *Nepenthes* secrete compounds that digest protein, but rather how to isolate, purify and characterize the protease(s) that exist. By this time, several characteristics of nepenthin were known: 1) Its activity is increased by acid conditions (*e.g.*, Gorup-Bensanez, 1874; Gorup-Bensanez and Will, 1876; Vines 1877, 1897; Zeeuw, 1934). 2) It does not degrade readily over time since pitcher extracts retained activity after two months (Vines, 1897). 3) The digestive activity is also unusually stable against heat and alkali (Vines, 1897). 4) The protease acts on a wide variety of substrates (Stern & Stern, 1932).

The Modern Era: 1964-Present

Previously, all the work characterizing the *Nepenthes* peptidase had demonstrated that the enzyme(s) present are endopeptidases, enzymes that cleave the middle of proteins. When endopeptidases have chopped proteins into smaller pieces, an exopeptidase is required to break off amino acids one by one off the short chains. Lüttge (1964b) showed that one kind of exopeptidase, leucine amino peptidase, was present in opened pitchers, but since it was not present in closed pitchers it was unclear if it was the product of contamination. Lüttge (1964b) also showed that digestive activity increased with temperature, peaking around 50°C or even as high as 60°C. The level of activity correlated with the Cl^- concentration in the pitcher (Lüttge, 1966), which strengthened the theory that the low pH in pitchers was due to hydrocloric acid (HCl) secretion.

Steckelberg *et al.* (1967) used chromatography to purify the *Nepenthes* protease to homogeneity. The activity of the purified enzyme from three species showed a

strong peak at pH 2.2 and had little activity above pH 4. Nakayama and Amagase (1969) purified the digestive enzyme using gel-filtration and column chromatography and proposed the name Nepenthesin for it. Again, the optimum pH was 2-3 and its heat stability was demonstrated up to temperatures as high as 60°C. They tested the direct effect of Cl^- ions on the enzyme activity and found that Cl^- had almost no effect up to concentrations of 10^{-3} M, but at concentrations higher than that (10^{-2} M) the effect was strongly inhibitory. Using several peptides of known structure they showed that the enzyme appears to cleave preferentially next to aspartic acid residues in the polypeptide chain with additional action on the carboxyl side of tyrosine and alanine. This was confirmed by Amagase *et al.* (1969). Amagase (1972) used electrophoresis to spread the enzymes in fluid from unopened and opened pitchers in a gel and then stained the gel for protease activity. Four separate bands (presumably each a different protease) were found in opened pitcher fluid. Three of these were also present in the fluid of unopened pitchers. The purified protease preparation, Nepenthesin, showed only one of these bands. Purified protease from *Drosera peltata* also had only one band in a similar location to the *Nepenthes* band, suggesting that the protease may be the same or similar in the two plants. Other characteristics of the *Drosera* protease (*i.e.* pH optimum, heat sensitivity and peptide cleavage patterns) were similar to those found for Nepenthesin.

Jentsch (1972) used repeated chromatography on ion exchange columns to isolate *Nepenthes* protease from sterile, unopened pitchers. He called it Nepenthacin. Lobareva *et al.* (1973) also purified the protease from *Nepenthes* and found that its activity was eliminated by a potent inhibitor (DDE) to the acid proteases of animals and fungi. This suggested that the active center of the enzyme in *Nepenthes* is functionally similar to that of animals and fungi. Takahashi *et al.* (1974) showed that two other potent inhibitors to acid proteases (DAN and pepstatin) also inhibit digestive activity in *Nepenthes*. Tökés *et al.* (1974) reported two proteolytic enzymatic fractions from unopened pitchers of *N. macfarlanei*. The major enzymatic activity appeared to be a protein of 59 kDa molecular weight while the minor fraction was around 21 kDa. No difference was found in opened pitchers, suggesting that no other protease is secreted after maturation. Studies using acid protease inhibitors on the activity of the 59 kDa protein corroborated the findings of Lobareva *et al.* (1973) and Takahashi *et al.* (1974). They also looked at the digestion products of the 21 kDa enzyme and found that it was different from that of Nepenthesin (which they equated with their 59 kDa enzyme). Their conclusion, however, that the 21 kDa enzyme "completes hydrolysis to free amino acids" does not seem to be convincingly demonstrated by the evidence they provide.

The acid protease was again purified by Athauda *et al.* (1998), this time from *N. distillatoria*. Using (presumably open) pitchers collected in the forests of Sri Lanka, they were able to purify about 2 mg of the protease from 30 l of fluid. They used a pepstatin-Sepharose column which specifically purified the protease. The molecular weight of the protease was measured as 45 kDa or 58 kDa by two different techniques, suggesting that it is the same or similar enzyme as the major fraction of Tökés *et al.* (1974). As with previous studies, they found the pH optimum between pH 2.0-3.0, a temperature optimum at 50-60°C and complete inhibition by pepstatin. Most interestingly, they report that the purified enzyme stains for carbohydrate. Jentsch (1970, 1972; Jentsch *et al.*, 1989) had complained about the difficulty in purifying *Nepenthes* protease due to interference by carbohydrate in the fluid, even in unopened pitchers. The findings of Athauda *et al.* (1998) suggest that Nepenthesin may be glycoprotein; that is to say, a protein modified with bound sugar molecules.

What is really new about Athauda *et al.* (1998) is that, for the first time, they report the amino acid sequence of part of the Nepenthesin molecule. Proteases exist in all life forms as part of an overall process of protein turnover (Ryan & Walker-Simmons, 1981). At the cellular level, organisms use proteases to break down proteins and reutilize them to support life processes. There are several classes of proteases present in plants and animals; Nepenthesin is an acid protease and is very

similar in function and character to the animal protease pepsin produced in the stomach. Athauda *et al.* (1998) state that, despite the functional similarity of Nepenthesin to other acid proteases, it has little homology (similarity of amino acid sequence) to the acid proteases from barley, rice and cardoon flower. In fact, the sequences of other known plant acid proteases show more homology to each other than they do to Nepenthesin. Athauda *et al.* (1998) conclude that Nepenthesin is a unique protease among plant and other acid proteases.

Even with all this evidence, the controversy continues as to whether the digestion in *Nepenthes* is effected by endogenous proteases. Tan and Ng (1997) cite unpublished work by Chia that digestion in young pitchers is accomplished via free radicals (reactive oxygen species such as H_2O_2, OH^-, and superoxide O_2^-) and not by endogenous proteases. Free radicals can digest protein, carbohydrate and lipids. They claim that free radical production increases with the maturity of the pitcher, peaking just after the lid opens, and declines thereafter. After the decline in free radical production, they argue, digestion of prey is effected by bacterial-derived enzymes. Santo *et al.* (1998) used photographic film placed in contact with gland tissues (see Heslop-Harrison & Knox, 1971; Hartmeyer, 1997) from *N. alata* to detect protease activity and claim that these glands do not secrete enzymes. They suggest that insect bacteria may be the primary digestive agent and that the glands appear specialized for nutrient uptake rather than digestion.

Conclusions

One hundred and twenty five years after Hooker first demonstrated the digestive ability of *Nepenthes* fluid, there is still a great deal we do not know about the process. I think the evidence is conclusive that *Nepenthes* produce and secrete an endogenous acid protease. We know that it is an enzyme relatively stable to heat, increased pH, and degradation over time (unlike the mammalian protease pepsin which it otherwise resembles) and that it is effective against a wide range of protein substrates. Specific qualities of this enzyme have led directly to much of the difficulties in its study. It is produced, most likely, only in small quantities; it is associated with carbohydrate and has a relatively low and narrow pH optimum. Studies performed at the ostensibly low pH of, say, 4.0 may still be too high to see significant action of the enzyme; pitchers with fluid pH above the optimum range may appear to be incapable of using Nepenthesin for digestion. It should be kept in mind, however, that the overall pH of pitcher fluid may not accurately reflect the true pH in the region of the glands where digestion and absorption occurs. Much of the confusion concerning *Nepenthes* digestion has revolved around the paradox of how to disentangle the role of any endogenous protease(s) from that of the digestive activity of microbes living in the pitcher fluid. Studying fluid from unopened pitchers may exclude bacteria, but a priori there is no reason to suppose that the enzyme is present or functional in closed pitchers since these are not yet capturing prey (some, but not all, studies have found the enzyme in unopened pitchers). On the other hand, studying digestion with fluid from opened pitchers will always be subject to the criticism that any digestion observed is really a function of microorganismic contamination, unless the plants are studied under sterile conditions *in vitro*.

Several questions about *Nepenthes* digestion are still unanswered. We do not know if the acid protease (nepenthesin) is produced first as a zymogen—an inactive precursor that is activated by low pH and the cleavage by existing protease (as is the case with pepsin). We do not know if there is more than one acid proteases produced by *Nepenthes* or if there are other kinds of proteases produced (such as exopeptidases). Another question that has scarcely been addressed is whether the acid protease(s) are in common to all *Nepenthes* species or if there might be significant differences among species. Is it possible some species forego endogenous production of proteases and let the microbes do all the work? Is the production of functional proteases disrupted in at least some hybrid taxa? Answers to such questions lie in the hands of future scientists or even enthusiastic laymen.

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